PALAEOZOIC CORAL FAUNAS FROM VENEZUELA, I. SILURIAN AND PERMO-CARBONIFEROUS CORALS FROM THE MÉRIDA ANDES

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CONTENTS

SYNOPSIS

Rugose and tabulate corals of Lower Llandovery, Ludlow and Permo-Carboniferous ages are described from localities in the southern part of the Mérida Andes of western Venezuela. The Palaeozoic stratigraphy of the area is briefly reviewed and the ages and relationships of the coral faunas are discussed. The new taxa *Columnaxon angelae* gen. et sp. nov., *Syringaxon arnoldi* sp. nov., *S. suripaense* sp. nov., *Streptelasma shagami* sp. nov., *Leolasma kaljoi* sp. nov. and *Cymatelasma aricaguaense* sp. nov. as well as species of *Lophophyllidium*, *Lophamplexus*, *Tryplasma*, *Coenites*, *Cystihalysites* and *Acanthohalysites* are described. Observations are made on the concepts of some genera and families, particularly *Syringaxon* and the Lindstroemiidae.

I. INTRODUCTION

The rugose and tabulate corals described in this paper come from localities in the southern part of the Mérida Andes of western Venezuela (Text-fig. 1). The bulk of the material was collected by H. C. Arnold (then Compañia Shell de Venezuela) during 1960–61 but additional material from R. Shagam (University of Pennsylvania) and G. R. Pierce and W. R. Smith (both Creole Petroleum Corporation) has been included. Faunas of three different ages are present; Lower Llandovery, Ludlow and Permo-Carboniferous (?Pennsylvanian), the latter two with some North American affinities. Sixteen species are described belonging to twelve genera; six species and one genus are new. Discounting preliminary reports all the genera except *Lophophyllidium* are recorded for the first time from South America. The material is housed in the Department of Palaeontology, British Museum (Natural History).

II. ACKNOWLEDGEMENTS

The author is grateful to Professor A. J. Boucot (Oregon State University), Dr J. G. Johnson (Oregon State University), Dr R. Shagam (University of Pennsylvania), Dr H. C. Arnold, Jr (Nederlandse Aardolie Maatschappij) and Dr J. M. Bowen (Shell International Petroleum Corporation) for discussion relating to the stratigraphy and age of the faunas from the Mérida Andes. Acknowledgement is also due to Compañia Shell de Venezuela and the Creole Petroleum Corporation for permission to describe this material which they have presented to the British Museum (Natural History).

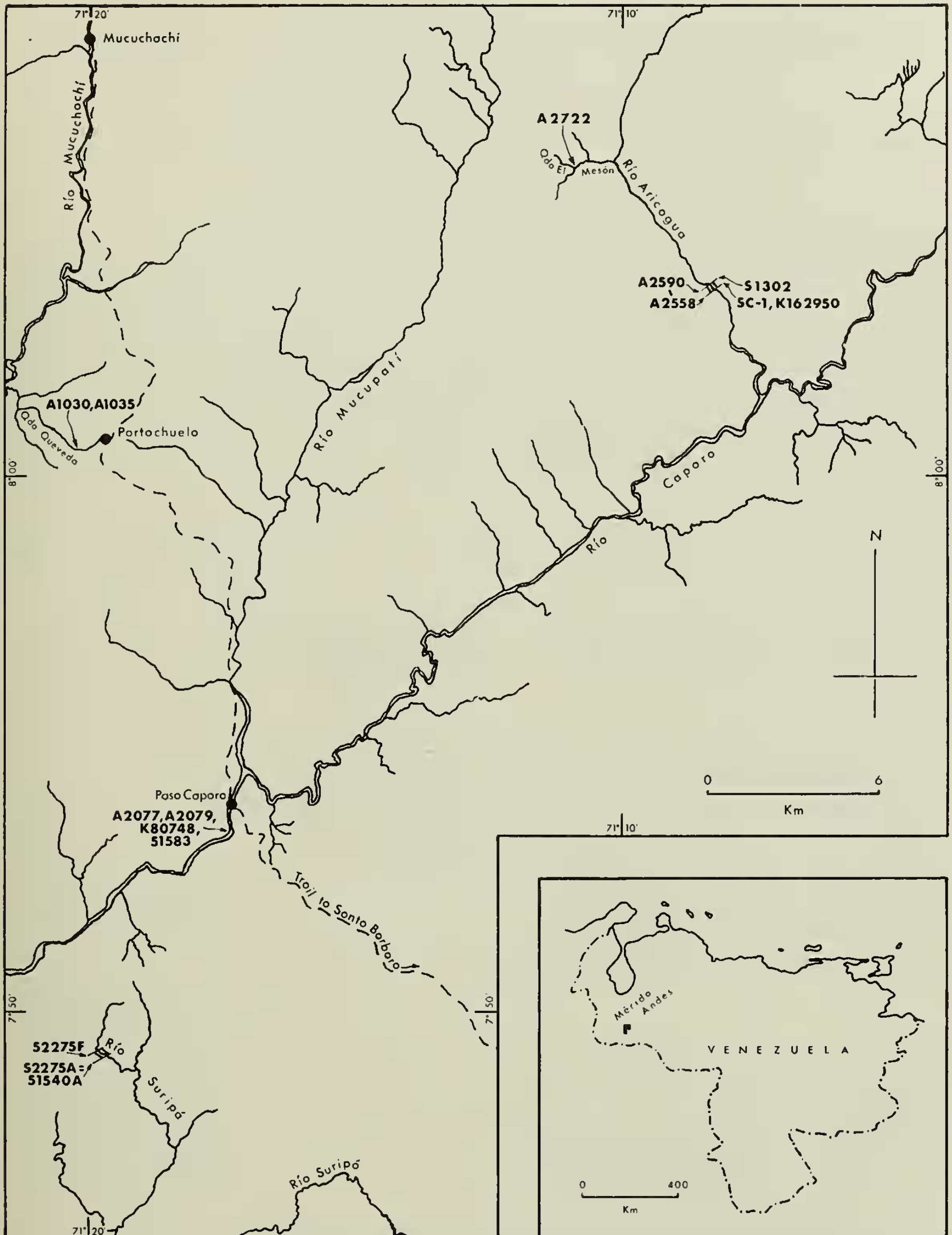

FIG. 1. Sample locations in the southern Mérida Andes. The area covered by the large scale map is indicated in the inset. For further explanation see Appendix.

Dr P. K. Sutherland (University of Oklahoma), and Dr W. J. Sando (United States Geological Survey) have kindly read and commented on the systematic section of the manuscript.

R. F. Wise and P. J. Green (both of the British Museum (Natural History)) respectively prepared thin sections and photographed material for this paper.

III. PALAEOZOIC STRATIGRAPHY OF THE SOUTHERN MÉRIDA ANDES

A review of the known Palaeozoic stratigraphy of the Mérida Andes was published by Cia. Shell de Venezuela & Creole Petroleum Corporation, 1964 (hereafter Shell and Creole, 1964). Their particular object was to demonstrate that the Devonian age assigned to the Mucuchachí Group by Pierce *et al.* (1961 : 352) was based on faunal misidentifications. The re-examination of the original material and of further collections made by H. C. Arnold shew faunas of Middle Ordovician, Silurian and Permo-Carboniferous age to be present in beds assigned to this group, but no

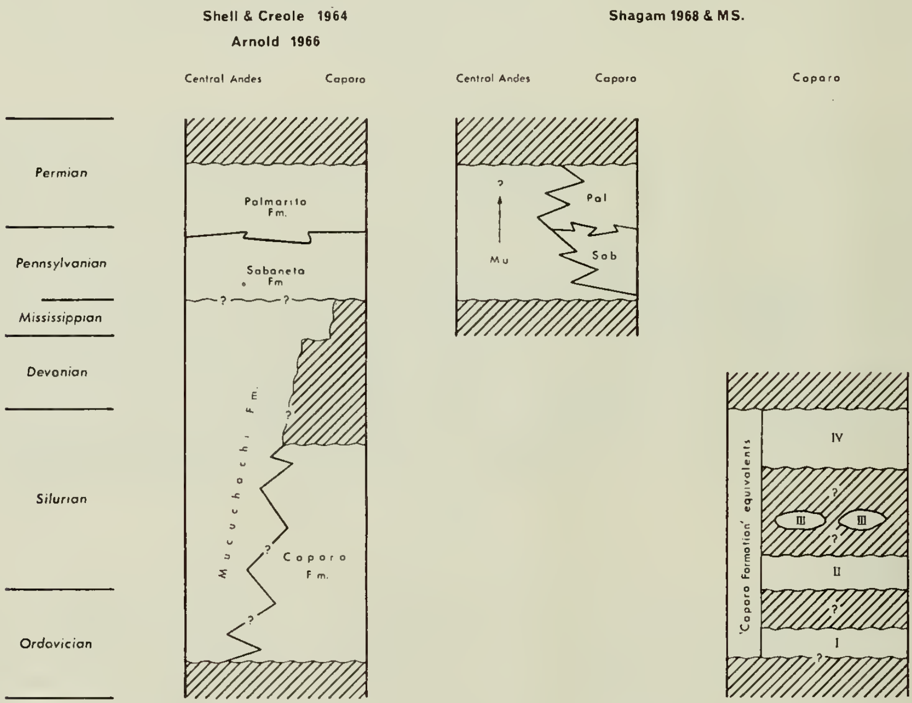

Fig. 2. Alternative interpretations of the Palaeozoic successions in the Mérida Andes, Venezuela. Pal = Palmarito Formation; Sab = Sabaneta Formation; Mu = Muchuchachí Formation. For comments see text.

evidence whatsoever of a Devonian fauna. They also shew that the Caparo Formation, previously considered Middle Ordovician (Schuchert 1935 : 692) and to underlie the Mucuchachí Group, contained faunas of Middle Ordovician to Upper Silurian age.

Pierce (1960 : 222; Pierce *et al.* 1961 : 350, 352) had recognized three formations in the Mucuchachí Group, the Remolino Formation, Libertad Formation and Río Momboy Formation in order of increasing age. Shell & Creole (1964 : 76), however, claimed that this division, based on erroneous palaeontological information, was inapplicable and unrecognizable in the field. They reassigned the Remolino Formation and part of the Libertad Formation to the Caparo Formation on field and faunal evidence. Thus, in their scheme, all known faunas of Middle Ordovician to Upper Silurian age occur in rocks assigned to the Caparo Formation and the only faunal evidence remaining for the restructured Mucuchachí Formation occurs 'high in the formation' (Shell & Creole 1964 : 83) and indicates a Permo-Carboniferous age.

Two possible interpretations of the spatial relationships of the Mucuchachí Formation were put forward (Text-fig. 2). H. C. Arnold considered the Caparo and the lower part of the Mucuchachí Formations to be distinct facies contemporaneously deposited in the same basin, whereas W. R. Smith related the Mucuchachí to the younger Palaeozoic sedimentary cycle including the Sabaneta and Palmarito Formations. Smith further thought that the older and younger Palaeozoic cycles were operative in geographically distinct basins. The latter viewpoint is also held by Shagam (pers. comm.) who postulates the lateral equivalence of the Mucuchachí and Sabaneta facies.

Shagam (1968 : 171) reported large limestone blocks containing a fauna of late Llandovery age embedded in supposed Wenlock—Ludlow shales in the Caparo area. This limestone, which presumably represents a fourth faunal horizon in Shell & Creole's so-called "Caparo Formation", is not yet known in its autochthonous situation. Shagam stressed the uncertainty surrounding much of the Lower Palaeozoic succession and expressed doubt as to its homogeneity. He postulated tectonic episodes between each of the four faunas so far recognized in this stratigraphical complex. To avoid the introduction of new stratigraphic units in this paper, which is primarily concerned with the coral palaeontology, the four faunal horizons in the Lower Palaeozoic rocks of the Caparo area are referred to by the roman numerals I (oldest) to IV (see Text-fig. 2).

In the Upper Palaeozoic sequence, the Palmarito Formation rests conformably on the Sabaneta Formation. The terrestrial red beds of the latter have yielded spores indicating a possible Permian age for most of the Sabaneta Formation according to Shell & Creole (1964 : 83) and Arnold (1966 : 2371) although the lower part may belong to the Carboniferous. The succeeding Palmarito is marine and richly fossiliferous but even so, the age of the formation is not precisely fixed. The macrofauna was considered by Pierce *et al.* (1961 : 357) to indicate a Pennsylvanian to Permian age, probably early Permian according to Arnold (1966 : 2378). Arnold (*op. cit.*), however, also reported preliminary ostracod identifications from the Palmarito of Quebrada Queveda as including many species comparable with Pennsylvanian ostracods of the U.S.A. In addition, the two corals described here from the Palmarito section of Quebrada Queveda both compare best with North American Pennsylvanian species. Thus the present faunal and floral evidence suggests that the Palmarito marine transgression began in Pennsylvanian times and was not completed in the area until the Permian. Clearly however, detailed studies of the Upper Palaeozoic sequences and their biota are needed here to determine more precisely the relationships of the various sedimentary units, both vertically and laterally.

IV. AGES AND RELATIONSHIPS OF THE CORAL FAUNAS

Very few systematic descriptions of Palaeozoic corals from South America have been published. The only previous work on Venezuelan material known to the writer is that of Weisbord (1926 : 224) which was revised by Wells (1943 : 95). This is all of Devonian age and will be referred to in more detail in a later paper dealing with faunas from the Sierra de Perijá. Other systematic work on South American Palaeozoic corals has been published by Douglas (1920 : 44), Knod (1908 : 561), Kozlowski (1923 : 97), Meyer (1914 : 601, 624) and Thomas (1905 : 267) but this only amounts to descriptions of about a dozen species. Mostly the same corals are also referred to in various fossil lists.

Almost all the genera and species described here, therefore, are either new or are recorded from South America for the first time. Three distinct coral faunas are present, two from the "Caparo Formation" equivalents of Lower Llandovery (Caparo II) and Ludlow (Caparo IV) ages respectively and one from the Palmarito Formation of Permo-Carboniferous (?Pennsylvanian) age.

(a) *"Caparo Formation" equivalents.*

(i) *Caparo II—Lower Llandovery.* A small collection of corals comes from a section on the Río Caparo approximately 900 m downstream from the Paso Caparo, the locality 2 of Shell & Creole (1964, tab. 1). Shell & Creole list two faunas from this locality, one probably middle Ordovician in age and the other early Llandovery. The corals, *Streptelasma shagami* sp. nov., *Leolasma kaljoi* sp. nov. and *Streptelasma* sp., are not sufficiently sensitive to indicate an age within these limits. *Leolasma*, it is true, has previously only been recorded from the upper Middle and lower Upper Ordovician of the Baltic and China but the range of the genus is felt to be far from adequately known. Ordovician and Silurian streptelasmids from North America are in need of extensive revision and no useful comparisons can be made there. On the other hand, brachiopods from the same samples as the corals are dated Lower Llandovery by J. G. Johnson (pers. comm.).

The corals described here are the *Streptelasma* spp., identified by H. D. Thomas and dated as Ordovician by him, which are listed by Shell & Creole (1964, table 1) under locality 2 as probably Ordovician.

(ii) *Caparo IV—Ludlow.* Several of the specimens described here were collected from a section on the Río Aricagua, the locality 7 of Shell & Creole (1964, table 1). Again, two faunas are listed, one collected by H. C. Arnold for Shell and dated Niagaran and the other collected by Creole and dated late Llandovery to Ludlow. Nearly all the corals are in five samples from the very detailed collections made by Arnold and appear to represent a single faunal suite. One specimen in the Creole collection and three specimens collected by R. Shagam from the same locality can be approximately equated with Arnold's samples (see Appendix) and also clearly belong to the same suite. The fauna contains *Syringaxon arnoldi* sp. nov., *Columnaxon angelae* gen. et sp. nov., *Cymatelasma aricaguaense* sp. nov. and *Cystihalysites brownsportensis* (Amsden). The presence of the latter suggests a younger Niagaran (Wenlock or early Ludlow) age, but unfortunately the new species are of no assistance and the genera are too long ranging to refine this age further. Brachiopods from the same samples as the corals indicate either Ludlow or Llandovery to Ludlow ages according to J. G. Johnson (pers. comm.). The homogeneity of the coral fauna suggests all the samples involved to be closely similar in age and thus a Ludlow horizon is indicated.

The fauna has one species in common with North American Silurian faunas. The genus *Cymatelasma,* however, has only previously been recorded from the Silurian of England, and the new genus and species make no contribution to an assessment of the faunal affinities.

A second fauna, also probably of Ludlow age, was collected by R. Shagam from a section on the Río Suripá. The corals are *Syringaxon suripaense* sp. nov., *Tryplasma* sp. cf. *T. nordica* Stumm, *Tryplasma* sp., *Coenites* sp., *Cystihalysites brownsportensis* and *Acanthohalysites* sp. Again a Wenlock or early Ludlow age is suggested by the presence of *C. brownsportensis*: *Tryplasma nordica* is also of Wenlock or Ludlow age. J. G. Johnson (pers. comm.) describes brachiopods from the same samples as probably Ludlow in age. The corals show some North American affinities but, more interestingly, *C. brownsportensis* is the only species in common between the Río Suripá and Río Aricagua faunas. This may be the result of small sample sizes, ecological variation or a slight difference in age between the two outcrops; it is not possible to decide which factor or combination of factors is responsible on the available evidence.

(b) *Palmarito Formation.*

Only four specimens from two localities are available from this formation. Two samples from the Portachuelo section (Qda. Queveda) yielded *Lophophyllidium pelaeum* (Jeffords) and *L.* sp. cf. *L. wewokanum* Jeffords. One sample from the Qda. El Mesón included *Lophophyllidium* sp. and *Lophamplexus* sp. *L. pelaeum* and *L. wewokanum* are both North American species of Pennsylvanian age whilst the *Lophophyllidium* sp. from the Qda. El Mesón is most similar to a North American species also of Pennsylvanian age. Thus there is some evidence here that the parts of the Palmarito Formation represented by these samples is Pennsylvanian rather than Lower Permian in age.

V. SYSTEMATIC DESCRIPTIONS

The terminology used in the following descriptions is that proposed by Smith (1945 : 4–9) and Moore, Hill & Wells (1956) unless otherwise indicated.

The sample number is given in brackets after the British Museum (Natural History), Department of Palaeontology registered number for each specimen. Sample numbers prefixed 'A' are from H. C. Arnold's collection, 'S' from R. Shagam's collection and 'K' from the collections of the Creole Petroleum Corporation. All available locality details for the samples are given in the Appendix. Comments on the locality and horizon of specimens in this section of the paper refer to broad units only (i.e. Río Aricagua section; Silurian, Ludlow) and reference should be made to the sample numbers in the Appendix for details.

Order RUGOSA Edwards & Haime 1850

Suborder STREPTELASMATINA Wedekind 1927

Superfamily **CYATHAXONIICAE** Edwards & Haime 1850

Family **LINDSTROEMIIDAE** Počta 1902

1902 Lindstroemiidae Počta : 181.
1962 Laccophyllidae; Philip : 170.
1965 Lindstroemiidae; Federowski : 336.
1965 Amplexocariniidae; Federowski : 350.
1965 Lindstroemiidae; Kullmann : 63, *pars*.
1967b Lindstroemiidae; Pedder : 110.
1967b Amplexocariniidae; Pedder : 124.
1968 Laccophyllidae; Goryanov : 90.

TYPE GENUS. *Lindstroemia* Nicholson & Thomson 1876 : 150.

DIAGNOSIS. Small solitary corals. Major septa fused at axis in early ontogeny to form a pseudocolumella. In some forms this persists in the mature stages, in others the septa are withdrawn to form a perfect or imperfect axial tube by the deflection, or by the thickening and lateral contiguity, of their axial ends. Minor septa contratingent when present, becoming free in the calice. Minor septa flanking counter septum accelerated; the remainder cyclically inserted in late ontogeny. Tabulae tent-shaped to box-shaped. Dissepiments developed in a few forms.

DISCUSSION. The type species of *Lindstroemia*, *L. columnaris* Nicholson & Thomson (1876 : 150) from the Devonian of North America, is imperfectly known and the type material cannot be traced. Nevertheless, as Pedder (1967b : 110) remarked, Nicholson & Etheridge (1878, text-figs 4b, 4b′ on p. 84) provided figures of the interior of *Lindstroemia columnaris* which justify the family concept and indeed caused Stumm (1949 : 7, 8) to suggest that *Lindstroemia* might prove to be a senior synonym of *Stereolasma* Simpson (1900 : 205).

The general characters of the corals assigned to this family have recently been discussed by Glinski (1963 : 323, 331), Fedorowski (1965) and Kullmann (1965 : 64

et seq.). Glinski (1963 : 331 *et seq.*) demonstrated the close relationship of *Svringaxon* to *Metriophyllum*, bringing these two genera together in the same family but distinguishing them at the subfamily level by the development of horizontal carinae in the Metriophyllinae. Pedder (1967b : 110), however, suggested that these carinae evolved independently in different lineages.

Fedorowski (1965 : 336, 342) recognized the subfamilies Metriophyllinae and Syringaxoninae based mainly on differences in the ontogeny of the aulos in those genera possessing one. He claimed that members of the Syringaxoninae form the earliest stages of the axial tube by the deflection of the axial ends of the major septa, as opposed to a slight withdrawal of the septa from the axis, without deflection, which produces the aulos in the Metriophyllinae. This account was apparently based in part on the ontogeny of specimens of *Syringaxon bohemica bohemica* (Barrande) from Poland. In the only other member of the Syringaxoninae described by Fedorowski (1965 : 344), *Stewartophyllum polonicum* (Sobolew), the ontogeny illustrated does not show a stage in which the aulos is formed by deflected septal ends, although he mentions other material belonging to this species which does. The writer has examined the sections cut by Butler to describe the ontogeny of *Syringaxon siluriense* (Butler 1935 : 120) and these also show no sign of such a stage in the development of the aulos.

The writer believes that the precise form of the axial ends of the septa in these corals is largely a function of aulos diameter, septal number and thickness and possibly the amount of sclerenchyme available to coat the axial structure. Septa remain straight throughout ontogeny in those corals where increase in aulos size is accompanied by a concomitant increase in the thickness of the septal ends as is shown by *Syringaxon siluriense* (BM(NH) R25891, R29444, R30165) and the specimen of *Stewartophyllum polonicum* figured by Fedorowski (1965, fig. 1D). In corals where increasing size of the axial structure is not matched by septal thickening, a tube is formed by deflecting the septal ends, as in the early stages of *Syringaxon bohemica bohemica* as figured by Fedorowski and such corals as '*Barrandeophyllum*' *perplexum* Počta (see Prantl 1938, pl. 3, fig. 16). Interpreted thus, no great significance is attached to the presence or absence of septal deflection in the construction of the aulos in the Lindstroemiidae.

Kullmann (1965 : 64) accepted Glinski's subfamilial division and diagnosed the Lindstroemiinae as exhibiting both cyclic and serial insertion of minor septa: he including the genus *Petraia* Münster in the subfamily. This he based on a reappraisal of the septal insertion in *Syringaxon* as illustrated by *S. siluriense* and two new species, *S. pinguis* and *S. postsiluriense*. The minor septa flanking the counter septum are inserted early in ontogeny, after the insertion of 14 major septa in *S. siluriense* (Butler 1935 : 121) and after 10 major septa in *S. pinguis* (Kullmann 1965, fig. 5). In the former, the rest of the minor septa are inserted in a normal cyclic manner when the number of major septa has reached 18, the average mature septal number in the species being about 20. Similarly, in *S. pinguis*, there are 14 major septa present before the rest of the minor septa are inserted more or less simultaneously, this being the average septal number in maturity. Butler (1935 : 122) regarded this basically as cyclic insertion of the minor septa, noting the early insertion of the two counter lateral minors and pointing out its occurrence in some other unrelated corals. Kullmann (1965 : 67) on the other hand, claimed that the situation in *Syringaxon* was homologous with that in *Petraia* in which minor septa are inserted serially with the metasepta from the earliest ontogenetic stages. The writer feels that Kullmann has considerably overstressed the significance of the early insertion of the counter lateral minor septa and that Butler's interpretation is the more reasonable. *Petraia* is excluded from the family Lindstroemiidae here.

Pedder's (1967b : 110) understanding of the Lindstroemiidae is essentially that accepted here. Fedorowski's (1965 : 350) removal of *Amplexocarinia* Soshkina to a new family, the Amplexocariniidae (followed by Pedder 1967b : 124), has been noted but the structure of the type species, *A. muralis* Soshkina, has yet to be clearly demonstrated. Otherwise both septa and tabulae appear to be involved in the formation of the aulos in species of *Amplexocarinia*, very like the development of this structure in such species as *Syringaxon memorabilis* Prantl (1938 : 30, pl. 1, figs 7, 8; pl. 2, figs 11, 12). Prantl described the aulos in *S. memorabilis* as formed by the bending of the axial ends of the major septa with only slight thickening, and unless the figure is misleading (pl. 3, fig. 11), the tabulae are developed with striking similarity to those illustrated in *A. tortuosa* by Fedorowski (1965, pl. 4, fig. 6). *Amplexocarinia* is retained in the Lindstroemiidae here.

Genus ***SYRINGAXON*** Lindström 1882

1882 *Syringaxon* Lindström : 20.
1900 *Laccophyllum* Simpson : 201.
1902 *Nicholsonia* Počta : 184.
1902 *Barrandeophyllum* Počta : 190.
1902 *Alleynia* Počta : [vi].
1928 *Laccophyllum*; Grabau : 82.
1928 *Alleynia*; Grabau : 84.
1928 *Barrandeophyllum*; Grabau : 87.
1935 *Syringaxon*; Butler : 117.
1938 *Syringaxon*; Prantl : 21.
1938 *Barrandeophyllum*; Prantl : 34.
1945 *Syringaxon*; Smith : 58.
1949 *Syringaxon*; Stumm : 10.
1949 *Barrandeophyllum*; Stumm : 10.
1951 *Syringaxon*; Schouppé : 207.
1954 *Syringaxon*; Schouppé : 395.
1956 *Syringaxon*; Flügel : 33.
1962 *Syringaxon*; Flügel & Free : 224.
1963 *Syringaxon*; Glinski : 331.
1965 *Syringaxon*; Sutherland : 34.
1965 *Syringaxon*; Fedorowski : 343.
1965 *Syringaxon*; Kullmann : 65.
1965 *Barrandeophyllum*; Kullmann : 87.
1968 *Syringaxon*; Goryanov : 91.
1968 *Barrandeophyllum*; Goryanov : 96.

Type species. *Cyathaxonia siluriensis* M'Coy 1850 : 281; 1851 : 36, pl. 1C, figs 11, 11a. High Bannisdale Slates or lowermost Kirkby Moor Flags (*vide* R. B. Rickards), Silurian, Ludlow, *leintwardinensis* zone; Underbarrow, near Kendal, Westmorland (see Pl. 1, fig. 6).

Diagnosis. Small simple, conical or cylindrical corals. A more or less perfect axial tube is formed in the late neanic and ephebic stages by the thickening and lateral contiguity or sideways deflection of the axial ends of the major septa. Minor septa usually developed, contratingent becoming free in the calice. No horizontal carinae but peripheral septal nodes present in some species. Tabulae horizontal in the axial tube and steeply sloping downwards to the periphery outside it; no dissepiments.

Discussion. Recent interpretations of *Syringaxon* have been based on Butler's (1935) paper in which he described in detail material he assigned to the type species, *S. siluriense*. Sutherland (1970) has now redescribed the holotype of *S. siluriense* (figured here on Pl. 1, fig. 6) which is clearly congeneric and almost certainly conspecific with Butler's material. Butler (1935 : 118) thought that both *Laccophyllum* Simpson and *Alleynia* Počta appeared to be synonyms of *Syringaxon* but he did not finally commit himself. Subsequently Prantl (1938 : 21) advocated the synonymy of *Alleynia* with *Syringaxon* on the basis of a comparison of the septal development in the two type species and Smith (1945 : 58, pl. 1, fig. 18) figured a syntype of *Laccophyllum acuminatum*, the type species of *Laccophyllum*, which is undoubtedly congeneric with *Syringaxon siluriense*.

Opinions have differed on the relationship between *Syringaxon* and *Barrandeophyllum*. Prantl (1938 : 34) reviewed earlier concepts of *Barrandeophyllum* and himself considered it worthy of generic status, distinguished from *Syringaxon* by the irregularity of its aulos, usually elliptical in section, by a sparing development of dissepiments and limited additional sclerenchyme. Prantl's dissepiments are actually the peripheral tabulae. Stumm (1949 : 10), Hill (1956 : 258) and Kullmann (1965 : 87) also consider the two genera distinct essentially on the same grounds. In addition, Stumm refers to a tendency in *Barrandeophyllum* for the diameter of the aulos to increase more rapidly with growth whilst Kullmann mentions the larger size and septal number and more numerous tabulae usually found in species of *Barrandeophyllum*.

Weissermel (1939 : 356; 1941 : 170), Schouppé (1951 : 207; 1954 : 396) and Flügel (1956 : 33) have all favoured a subgeneric relationship. Schouppé claimed the presence of 'dissepimental interconnexions' between the septa in *Barrandeophyllum* as taxonomically significant but Flügel & Free (1962 : 231) quite rightly point out that these are merely sections of tabulae which tend to be more numerous in species assigned to *Barrandeophyllum* than in those assigned to *Syringaxon*.

Only Wang (1950 : 204) and Flügel & Free (1962 : 224 *et seq.*) have placed *Barrandeophyllum* in synonymy with *Syringaxon*. Flügel & Free expressed reservations, however, and recorded (1962 : 231, footnote 2) an apparent difference between the septal microstructure developed in a specimen of *B. bohemicum* and that in their species of *Syringaxon*. This is considered here in all probability to be due to the effects of recrystallization in the latter material.

Thus all characters that have been quoted as distinguishing *Barrandeophyllum* from *Syringaxon* have either been misinterpreted or are of a quantitative nature. There appears to be no basic structural divergence to warrant separation at the generic level. Differences in size, growth-form and degree of perfection in the formation of the aulos are here considered to be of specific significance only and *Barrandeophyllum* is therefore placed in synonymy with *Syringaxon*.

Syringaxon arnoldi sp. nov.

(Pl. 1, figs 1–5; Text-fig. 3)

Derivation of name. After the collector, Dr H. C. Arnold, Jr of Nederlandse Aardolie Maatschappij.

Diagnosis. *Syringaxon*, 4·1 to 5·1 mm diameter with 15 to 18 major septa at base of calice. Minor septa contratingent; counter-lateral minor septa equal in length to counter septum, others half radius in length. Aulos wide but with narrow axial tube largely infilled in pre-ephebic stages. Tabulae sparse within aulos and rare outside it.

Holotype. R46740 (A2558). Río Aricagua section; Silurian, Ludlow.

Paratypes. R46741–2 (A2561), R46743–4 (A2582), R46745 (K162950). Same locality and horizon as holotype.

Description. Small, conico-cylindrical corals up to 6 mm in diameter and 10 mm in length. Epitheca with strong inter-septal ridges.

In cross-section, uncrushed corals are circular with a longitudinally corrugated epitheca and a peripheral stereozone 0·3 to 0·4 mm thick. At the base of the calice, the major septa extend almost to the axis where their thickened, club shaped ends are more or less laterally contiguous and invested in sclerenchyme to form a regular, thick walled aulos 1·4 to 1·7 mm in diameter. There is no deflection of the septal ends in the aulos which has a maximum internal diameter of 0·8 mm. The major septa are waisted between the aulos and the outer wall, thinning to 0·15 mm or less across with the cardinal septum almost invariably thinner than the other major septa. The minor septa are contratingent and usually reach half the coral radius in length: the counter-lateral minor septa are equal in length to the counter septum.

Above the calice base, the aulos degenerates first on the cardinal side and lastly on the counter side. The major septa begin to withdraw peripherally and the minor septa become free at their axial ends 0·5 mm above the first breach in the aulos: 2 mm above the base of the calice, the septa are reduced to ridges up to 0·5 mm in length and virtually inseparable into major and minor series.

In longitudinal section, the aulos is largely infilled in pre-ephebic stages, leaving scattered axial bowl or funnel shaped voids capped by shallowly depressed tabulae in the neanic stage. Between the aulos and the peripheral stereozone, one tabula sloping axially and upwards was seen in the region of the counter septum in the holotype (Pl. 1, fig. 2). On the cardinal side, three arched plates are present at the periphery but their form towards the aulos is obscured by septa in the plane of section. Signs of tabulae are extremely rare in the paratypes.

At the base of the calice, the corals vary in diameter between 4·1 and 5·1 mm with 15 to 18 major septa. Septal ratios vary between 3·3 and 3·7. The measurements are plotted in Text-fig. 3.

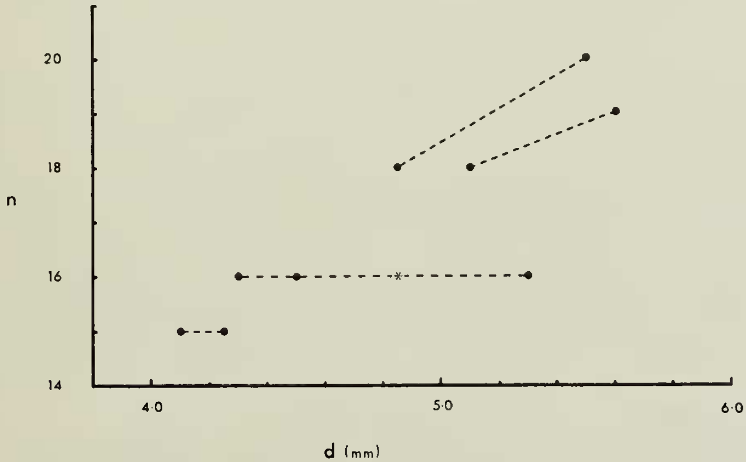

Fig. 3. Number of major septa plotted against diameter for specimens of *Syringaxon arnoldi*. The holotype is indicated by an asterisk. The dashed lines join points representing different sections of the same specimen.

Discussion. *Syringaxon arnoldi* is easily distinguished from the North American species *S. acuminatum* (Simpson) by the much larger thin walled aulos, thin septa and well developed tabulae in the latter. *S. adaense* Sutherland (1965 : 34) from the Henryhouse Formation of Oklahoma is also clearly distinct, through its extremely short minor septa in particular. *Syringaxon arnoldi* resembles most closely the German Eifelian species *S. wedekindi* Glinski (1963 : 331, fig. 5) although it is difficult from the cursory description and drawing to make a proper comparison. *S. wedekindi* apparently has a septal ratio of 2·7, considerably less than that for *S. arnoldi*, and the detailed septal shape, with a strong peripheral expansion, is distinctive.

Syringaxon suripaense sp. nov.

(Pl. 1, figs 7, 8; Text-fig. 4c)

Derivation of name. After the type locality on the Río Suripá.

Diagnosis. *Syringaxon*, 5·0 to 5·7 mm in diameter with 18 to 19 major septa at base of calice. Minor septa contratingent; counter-lateral minor septa equal counter septum, others half radius or slightly more in length. Nodes present on major and minor septa close to periphery. Aulos medium to thin walled, may be irregular in shape.

HOLOTYPE. R46746 (S2275D). Río Suripá section; Silurian, Ludlow.

PARATYPE. R46747 (S2275D). Same locality and horizon as holotype.

DESCRIPTION. Two fragments of small solitary corals embedded in grey mudstone. External shape unknown.

In cross-section, the corals are subcircular with a strongly longitudinally corrugated epitheca reflecting pronounced interseptal ridges. The peripheral stereozone is 0·2 mm thick. The major septa are thin, about 0·15 mm across, and reach within a short distance of the axis at the base of the calice. The axial ends of the septa have a pronounced club-shaped thickening bringing them into lateral contact to form a medium to thin walled aulos. There is little additional material reinforcing the structure. The aulos may be regular or irregular in shape and has an internal diameter of about 0·8 mm. The minor septa are the same thickness as the major septa and contratingent with them. They may reach 0·6 of the radius in length except for the counter-lateral minor septa which are equal in length to the counter septum. Both major and minor septa develop irregular rounded or sharp edged nodes (Knoten of Kullmann 1965), 0·5 mm from the epitheca, which may double or treble the normal septal thickness. The nodes partially close the space between adjacent major septa to produce a keyhole appearance at the peripheral end of the gap (see particularly Pl. 1, fig. 7 and Text-fig. 4c).

No longitudinal sections of the species are available. Signs of tabulae between the major septa in cross-section are extremely rare although sections of horizontal elements appear more commonly between the major septa and their contratingent minors.

Coral diameters at the base of the calice are 5·0 mm with 18 major septa and 5·7 mm with 19 major septa. Septal ratios are 2·8 and 3·0.

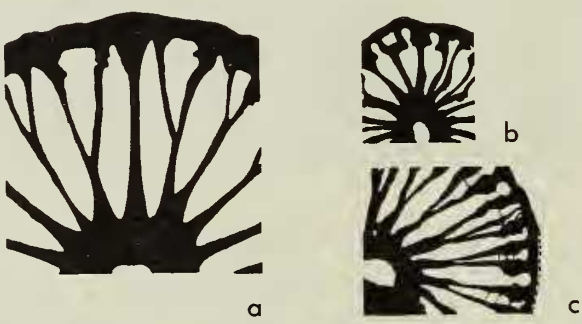

FIG. 4. The development of septal nodes in species of *Syringaxon*; a. *S. cantabricum*, b. *S. parvum*, c. *S. suripaense*. Figs 4a and 4b after Kullmann (1965, text-figs 7d, e). All × 8.

DISCUSSION. The development of septal nodes distinguishes *S. suripaense* from all syringaxoniids but two species assigned to *Barrandeophyllum* by Kullmann (1965 : 88, 91), *B. cantabricum* and *B. parvum* from the Emsian of North Spain (see Text-fig. 4). *B. cantabricum,* however, is a much larger species, reaching 13 mm in diameter. The septal nodes take a slightly different form from those of the Venezuelan material and the counter-lateral minor septa are significantly shorter than the counter septum. *B. parvum,* on the other hand, is more similar to *S. suripaense* although somewhat smaller and distinguished by a very small aulos.

Genus ***COLUMNAXON*** nov.

DERIVATION OF NAME. Descriptive of the axial columella characteristic of the genus.

DIAGNOSIS. Very small, simple, conico-cylindrical corals. Aulos present in early ontogeny. In ephebic stage, counter septum forms a columella against which other major septa abut to form a solid axial column. In the calice, major septa withdraw, the counter septum last, to leave a free columella. Minor septa contratingent at calice base, free in calice; counter-laterals accelerated. Tabulae simple, sloping down from axial structure to periphery and flat within aulos of early ontogeny.

TYPE SPECIES. *Columnaxon angelae* sp. nov.

DISCUSSION. *Columnaxon* is essentially *Syringaxon* in which, in the ephebic stage, the counter septum grows into the aulos and dilates to close the axial tube. This columella formed by the counter septum persists into the calice and becomes isolated by the withdrawal of the major septa, finally severing contact with the counter septum to form a free standing boss or spine.

This structural modification of *Syringaxon* is interesting as the result is strongly homoeomorphic with the Carboniferous genus *Cyathaxonia.* The columella in *Cyathaxonia,* however, is formed independently of the major septa and not as a dilation of the axial end of the counter septum as in *Columnaxon.* Also, minor septa in *Cyathaxonia* are inserted alternately with the major septa. In *Columnaxon* the septal insertion is not known but is thought to be the same as in *Syringaxon* which is, with the exception of the accelerated counter-lateral minors, cyclic. *Columnaxon* also shows a gross homoeomorphy with *Lophophyllidium.* The latter genus, however, lacks the strongly accelerated counter-lateral minor septa of *Columnaxon* and possesses a weak cardinal septum in a distinct fossula.

Columnaxon angelae sp. nov.

(Pl. 1, figs 9–12; Text-fig. 5)

DIAGNOSIS. *Columnaxon* 9 mm long, 5·5 mm maximum diameter with 16 major septa.

HOLOTYPE. R46748 (A2579). Río Aricagua section; Silurian, Ludlow.

ADDITIONAL MATERIAL. R46749 (SC1), R46750 (S1302). Same locality and horizon as holotype.

DESCRIPTION. Small, straight, conico-cylindrical coral, 9 mm long and 5·5 mm maximum diameter. There are 16 major septa.

In cross-section, the coral is circular with a longitudinally corrugated epitheca reflecting strong interseptal ridges. A peripheral stereozone 0·5 mm thick is developed. Midway to the axis, the counter and cardinal septa are about 0·1 mm thick and the other major septa about 0·2 mm thick. The septa expand gradually towards the periphery. In the sub-calicular sections, all major septa except the counter reach 0·85 of the radius in length. Their axial ends are dilated and in lateral contact, forming, with a little additional sclerenchyme, a strong periaxial wall. The counter septum, however, extends through the wall to the axis with a considerably expanded, club shaped end about 0·5 mm across which more or less completely blocks the axial tube (see Text-fig. 5g). Evidence from the longitudinal section suggests that in early ontogeny a more normal aulos may be present and that the counter septum does not grow into the axis until the late neanic or early ephebic stage (see Pl. 1, fig. 9).

In the sub-calicular section the minor septa are about half the radius in length and contratingent. The counter-lateral minors, however, are very nearly as long, three-quarters of the radius, as the major septa (excepting the counter), although notably thinner.

At the base of the calice, the major septa withdraw from the axis first in the cardinal area and last in the counter area (Text-fig. 5). Minor septa also become free standing first adjacent to the cardinal septum and progressively later towards the counter. The counter-lateral minor septa are an exception and detach from the counter at about the same level as the minor septa in the alar area become free.

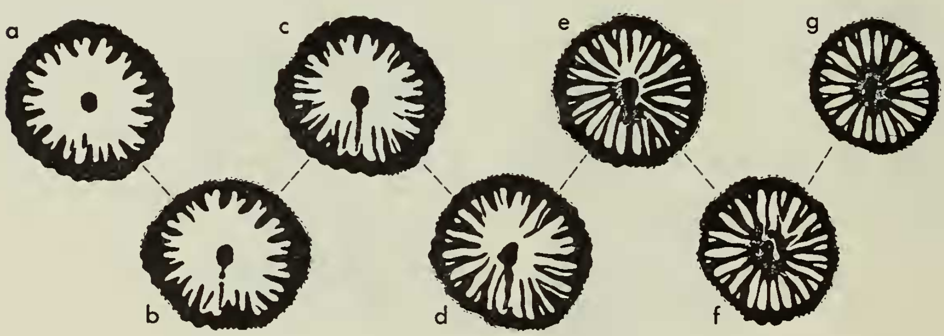

FIG. 5. Late stage development in the holotype of *Columnaxon angelae*. Spacing of cross-sections: a (R46748a)—0·6 mm—b (R46748b)—0·6 mm—c (R46748c)—0·6 mm—d (R46748d)—1·2 mm—e (R46748f)—1·8 mm—f (R46758i)—1·2 mm—g (R46748k). All × 4.

The counter septum becomes uniformly thin from the periphery to the sharply defined quadrate columella slightly elongated in the counter-cardinal plane and 0·75 × 0·6 mm in section. Finally, the counter septum withdraws very rapidly leaving the columella, now 0·7 × 0·5 mm, isolated in the axis. It is not known how much higher in the calice the columella extends.

In the longitudinal section (Pl. 1, fig. 9), the axial column is solid and about 1·6 mm wide in the distal (late neanic—early ephebic) 0·7 mm. Below this, however, a bowl-shaped void is capped by a flat, slightly inclined tabula indicating that an aulos is open at this stage of ontogeny. The column decreases in width proximally and a very fine axial canal, in which traces of tabulae can be seen, is present in the lower 1·5 mm preserved: the tip of the coral has been eroded. The interseptal spaces outside the axial structure appear to be poorly partitioned. Traces of two, or possibly three tabulae are visible on the counter side, concave up peripherally and apparently directed axially and upwards to the core, although towards the centre a septum in the plane of section obscures them.

Discussion. This description is based on the holotype alone as the two other specimens of *Columnaxon* available cannot be confidently assigned to the same species. R46749, 3·8 mm in diameter with 15 major septa, may represent a slightly earlier ontogenetic stage than any seen in the holotype with the aulos only partially infilled by the counter septum. It has, however, rather distinctive axial thickening of the major septa. R46750, on the other hand, is a calicular section 3·7 mm in diameter with 14 major septa. It has a thin (0·2–0·25 mm) peripheral stereozone which is highly crenulate and a very elongate columella 1 × 0·3 mm in section. The holotype at a comparable stage of development is 5·3 mm in diameter with 16 major septa. These may be variants of the same species or taxonomically distinct and a decision is best left until additional material allows specific variation to be assessed.

Family **LOPHOPHYLLIDIIDAE** Moore & Jeffords 1945

Genus ***LOPHOPHYLLIDIUM*** Grabau 1928

1928 *Lophophyllidium* Grabau : 98.
1928 *Sinophyllum* Grabau : 99.
1941 *Lophophyllidium*; Moore & Jeffords : 78.
1942 *Lophophyllidium*; Jeffords : 211.
1945 *Lophophyllidium*; Moore & Jeffords : 93.
1947 *Lophophyllidium*; Jeffords : 15, 21.
1947 *Stereostylus* Jeffords : 16, 38.
1953 *Lophophyllidium*; Formichev : 180.
1953 *Agarikophyllum* Formichev : 196.
1955 *Lophophyllidium*; Minato : 151.
1961 *Lophophyllidium*; Fontaine : 77.
1961 *Sinophyllum*; Fontaine : 79.
1961 *Khmerophyllum* Fontaine : 81.
1961 *Stereostylus*; Fontaine : 83.
1962 *Lophophyllidium*; Ross & Ross : 1181.

1962 *Stereostylus*; Ross & Ross : 1185.
1964 *Lophophyllidium*; Rowett & Sutherland : 25.
1966 *Stereostylus*; Bebout : 1.

TYPE SPECIES (original designation). *Cyathaxonia prolifera* McChesney 1860 : 75 and 1865, pl. 2, figs 1–3. Upper Pennsylvanian, 8 miles south of Springfield, Illinois, U.S.A.

DIAGNOSIS. Solitary corals possessing a columella formed by the expansion of the axial end of the counter septum from which it may separate in the ephebic stage. Major septa except cardinal long and usually rhopaloid. Tabulae tent-shaped; no dissepiments.

DISCUSSION. The lophophyllidid corals were extensively reviewed by Moore & Jeffords (1941, 1945) and Jeffords (1942, 1947). The writer follows Duncan (1962 : 65) and Rowett & Sutherland (1964 : 25) in considering slight structural differences in the columella and the degree of thickening of the skeletal elements in these corals not to be of generic significance. Thus, in agreement with them, *Stereostylus* is placed in synonymy with *Lophophyllidium*. The subgenus *Agarikophyllum* Formichev (1963) and the genus *Khmerophyllum* Fontaine (1961) have also been erected on supposedly significant modifications of columella structure. In both cases, however, generic differentiation from *Lophophyllidium* is thought not to be warranted.

Lophophyllidium has been recorded several times previously from South America —from the Permian of Bolivia (see Ahlfeld & Braniša 1960 : 100) and from the Carboniferous of Peru by Douglas (1920 : 44). It has unfortunately not proved possible to compare the present material with these earlier records.

Lophophyllidium pelaeum (Jeffords 1947)

(Pl. 1, figs 13–15)

1947 *Stereostylus pelaeus* Jeffords : 48, fig. 7, pl. 16, figs 1–8, pl. 20, figs 1 and 7.
1966 *Stereostylus brushensis* Bebout : 3, pl. 2, figs 1–3.

MATERIAL. R46751 (A1030). Qda. Queveda section; Permo-Carboniferous (?Pennsylvanian).

DESCRIPTION. Small conical coral, outer form uncertain but epitheca with strong septal grooves.

In the late neanic stage, the peripheral stereozone averages 0·5 mm thick. The major septa are slim, 0·2–0·25 mm across at their narrowest, and usually very slightly rhopaloid, their axial ends fused about two prominent alar fossulae (Pl. 1, fig. 13). The counter septum is not clearly distinguished but comparable in length with adjacent septa. The cardinal septum is slightly shorter than its adjacent septa but no pronounced cardinal fossula is present. In septal formula is $C3A10K9A4C$ at a diameter of 10 mm. Minor septa may be present as rudimentary swellings between some of the major septa. Tabulae are intercepted quite frequently.

In the ephebic stage (Pl. 1, fig. 14), the peripheral stereozone is thinner, 0·3–0·5 mm thick. All septa except the counter are variably withdrawn from the axis. The cardinal septum is very short, 1·5 mm in length, tapering to a point in a narrow, key-hole shaped cardinal fossula. Other major septa are 0·15 mm thick, weakly rhopaloid and vary in length between two-thirds and almost the full radius. The counter septum extends to the axis with a rhopaloid end, no clear cut column being formed. The septal formula is not clear; there are 31 major septa at a mean diameter of 12 mm. Minor septa are developed only in the counter quadrants, increasing in length towards the counter septum. Only one tabula is cut in this section and shows strong axial displacement in the cardinal fossula.

The longitudinal section is cut slightly off centre and septa obscure some of the details. The tabulae are thin, largely complete, well spaced and slope steeply axially and upwards in the peripheral areas.

Discussion. The Venezuelan specimen agrees very closely with *Stereostylus pelaeus* Jeffords from the Missourian (Upper Pennsylvanian) of Oklahoma and Kansas. *S. brushensis* Bebout is slightly smaller than *S. pelaeus* but otherwise does not appear to differ significantly from that species. *S. bruhsensis* is recorded from the Conemaugh of Ohio which is correlated with the Missourian of the mid-continental U.S.A.

Lophophyllidium sp. cf. ***L. wewokanum*** Jeffords 1947

(Pl. 1, figs 16–18)

cf. 1947 *Lophophyllidium wewokanum* Jeffords : 24, figs 5, 6; pl. 4, figs 4–7; pl. 7, fig. 5; pl. 10, figs 4–5; pl. 11, fig. 3.
?cf. 1947 *Lophophyllidium plummeri* Jeffords : 33, figs 1, 5–6; pl. 5, fig. 4; pl. 7, figs 2, 6, 7; pl. 10, figs 2, 3; pl. 11, figs 1, 2, 5, 6.

Material. R46752 (A1035). Qda. Queveda section; Permo-Carboniferous (?Pennsylvanian).

Description. Conical coral of 15 mm maximum mean diameter with strong septal grooves.

The peripheral stereozone is largely beekitized but about 0·8 mm thick. In the section immediately below the calice (Pl. 1, fig. 18), the septa are moderately thick, 0·3–0·4 mm across at their mid point, expanding slightly to the periphery and rhopaloid. Apart from the cardinal septum, the major septa are slightly variable in length around 0·7 of the radius. The counter, counter-lateral and alar septa may just touch the columella which is large, oval to quadrate and measures 2·6 × 2·4 in cross-section. There is a discontinuity between the counter septum and the columella. The cardinal septum is very short, less than half the radius, in a quadrate fossula formed by the slightly pinnate arrangement of the cardinal quadrant septa. The septal formula is $C5A7K7A4C$ at a diameter of 12 mm. Minor septa are not apparently developed at this level. Tabulae appear widely spaced, regularly concentric except in the cardinal fossula where they are displaced axially. The microstructure is obscure, many septa showing a chevron pattern which is probably the result of recrystallization.

In the base of the calice, the columella is oval and smaller, 2·6 × 2·1 mm, with its long axis in the counter-cardinal plane. Its reduction in size is continued quite rapidly as at a low level in the calice, with the major septa still two-thirds the radius in length and with the counter septum still abutting the columella, its dimensions are 2·5 × 1·75 mm (Pl. 1, fig. 16). Minor septa begin to appear at the base of the calice but remain as little more than low ridges. The cardinal septum shortens and projects only 1 mm from the wall in the base of the calice. The number of major septa increases from 27 at a diameter of 12 mm just below the calice to 29 at a mean diameter of 13·5 mm in the calice itself.

The longitudinal section is dominated by the broad axial columella. The tabulae are thin, mostly complete, generally flat and steeply sloping axially and upwards towards the columella, flattening out in the axial area. They are often crested in part by septal material. On the cardinal side, what appear to be growth-lines in a septum partly in the plane of section are broadly trough shaped between the periphery and columella.

Discussion. The Venezuelan specimen has features in common with *Lophophyllidium wewokanum* Jeffords from the Desmoinesian of Oklahoma and *Lophophyllidium plummeri* Jeffords from the Virgilian of Texas. In fact, it would appear that Jeffords (1947 : 34) only distinguished these two species on the basis of their stratigraphical separation and a purely morphological distinction between them would be very difficult to maintain. The present specimen differs from them in a number of small points such as the quadrate cardinal fossula, the diminution of the columella in the lower calice whilst still contiguous with the counter septum and the weaker minor septa. Both *L. wewokanum* and *L. plummeri* have triangular fossulae and large isolated columellae in the lower calice, and *L. plummeri* has quite well developed minor septa.

Lophophyllidium sp.

(Pl. 2, figs 1, 2)

Material. R46753 (A2722). Qda. El Mesón section. Permo-Carboniferous (?Pennsylvanian).

Description. Corallite shape is unknown but the epitheca develops shallow septal grooves.

At the base of the calice (Pl. 2, fig. 1), the peripheral stereozone is 0·4 mm thick. The major septa are slim, expanding slightly towards the periphery and weakly rhopaloid. They are withdrawn from the axis, the alars about 0·6 of the radius in length, and the other major septa shorter and slightly variable in length. The cardinal septum and the two flanking major septa are very short with tapering axial ends leaving a rather wide cardinal fossula. The counter septum extends towards the axis with a slim spindle shaped dilatation. The thin axial end then joins the columella at one side and appears to be partly wrapped round it. The columella is slim and oval, 2·3 × 1·2 mm in section, elongated in the counter-cardinal plane. The septal formula is *C6A7K7A7C* at a diameter of 12 mm. Minor septa are very short and thorn-like. The tabulae appear widely spaced.

A section in the calice, with 32 major septa at a diameter of 13 mm, shows a strong isolated columella 2·2 × 0·9 mm in section with the major septa, including the counter, smoothly tapered and half the radius or slightly less in length. The cardinal septum is reduced to one-fifth the radius with the two flanking major septa slightly longer. The minor septa are short but evenly developed.

No longitudinal section is available.

DISCUSSION. This specimen compares most closely with *Lophophyllidium elongatum* Jeffords (1942 : 234, pl. 4, figs 1–3) from the Missourian (Upper Pennsylvanian) of Oklahoma. There seem to be too many distinctions in detail, however, for the Venezuelan specimen to be assigned to this species. *L. elongatum* varies between 10·3 and 19 mm in diameter with 28 to 30 major septa accelerated in the counter quadrants, with very long major septa in the base of the calice and a narrow triangular fossula. The specimen described here has a higher septal ratio and lacks the acceleration of the counter quadrant normally so characteristic of the lophophyllidiids. Also, the major septa are shorter than in *L. elongatum* and the two septa flanking the cardinal septum are noticeably reduced in length.

Genus ***LOPHAMPLEXUS*** Moore & Jeffords 1941

1941 *Lophamplexus* Moore & Jeffords : 90.
1945 *Lophamplexus*; Moore & Jeffords : 120.
1947 *Lophamplexus*; Jeffords : 62.

TYPE SPECIES (original designation). *Lophamplexus eliasi* Moore & Jeffords 1941 : 91, pl. 3, figs 2, 3; pl. 8, fig. 1. Lower Permian (Wolfcampian); Grand Summit, Cowley County, Kansas, U.S.A.

DIAGNOSIS. Solitary corals, possessing a columella formed by the expansion of the axial end of the counter septum in early stages, which becomes discontinuous or is lacking in maturity. Major septa much shortened and cardinal fossula indistinct in mature stages. Minor septa may be weakly developed. Tabulae simple tent-shaped or flat-topped domes; no dissepiments.

DISCUSSION. *Lophamplexus* does not appear to have been recorded before outside North America where it is known from the Pennsylvanian and Lower Permian.

Lophamplexus sp.

(Pl. 2, figs 3–6)

MATERIAL. R46754 (A2722). Qda. El Mesón section. Permo-Carboniferous (?Pennsylvanian).

Description. Slim, conical coral with very weak septal grooves.

In the late neanic stage (Pl. 2, fig. 3), the major septa are slim and taper gently to meet at the axis in the counter quadrants, with the counter septum itself slightly rhopaloid. In the cardinal quadrants, the septa are variably withdrawn from the axis leaving a large cardinal fossula in which the cardinal septum is slightly longer than the flanking septa. The tabulae appear quite closely spaced. The diameter is about 9 mm with 27 major septa.

In the early ephebic stage (Pl. 2, fig. 4), the peripheral stereozone is 0·4–0·5 mm thick. The major septa are very variable in length, between one-third and two-thirds the radius. The counter septum, however, extends to the axis and is weakly rhopaloid. The cardinal septum which is half the radius in length is flanked by very short major septa. Traces of minor septa are present between most major septa and are particularly well developed either side of the cardinal septum. Tabulae appear closely spaced at the periphery but leave a clear axial area. The diameter is 10 mm with 27 major septa.

In higher sections (Pl. 2, fig. 5) the counter septum also withdraws from the axis, leaving an axial area one third to one half the diameter across free of septa. Several major septa, including the counter septum may develop rhopaloid ends. At the base of the calice the diameter is 11 mm with 30 major septa.

The longitudinal section is cut from the proximal part of the corallite and shows a strong axial core which appears to involve several septa in the plane of section. The tabulae are strong, generally complete and slope steeply axially and upwards flattening slightly near the axis.

Discussion. This specimen cannot be assigned to a described species of *Lophamplexus* at the moment and may prove to be a new species. Further material is required, however, to furnish information not available from the present specimen and to determine if certain characters, such as the relatively long cardinal septum, are consistently maintained.

Superfamily **ZAPHRENTICAE** Edwards & Haime 1850

Family **STREPTELASMATIDAE** Nicholson 1889

1956 Streptelasmatinae; Hill : 268, *pars.*
1965 Streptelasmatidae; Kullmann : 139.
1969 Streptelasmatidae; Neuman : 7.

Type genus. *Streptelasma* Hall 1847 : 17.

Diagnosis. Solitary corals with a narrow peripheral stereozone. Axial ends of major septa either lobed or discontinuous and usually involved in a loose axial structure, or amplexoid in ephebic stages. Cardinal fossula may or may not be distinguished. Tabulae generally complete; arched. No dissepiments.

Discussion. Ivanovskii (1965 : 57) has divided the Streptelasmatinae of Hill (1956 : 268) among three families mainly on the basis of the development of stereoplasm and septal thickening in early ontogeny. Whilst these factors have in some cases played a part in the diagnosis of streptelasmatid genera, divisions at family level are more soundly based on major structural modifications which are considered to have phylogenetic significance. Skeletal thickening alone in the streptelasmatids does not appear to be of fundamental taxonomic importance and Ivanovskii's scheme cuts across more natural relationships. For example, *Streptelasma*, *Crassilasma* and *Dinophyllum* are all placed in separate families despite their basic structural similarities; similarly *Leolasma* and *Kenophyllum*.

Kullmann (1965 : 140), on the other hand, recognized two groups within the Streptelasmatinae of Hill. He separated off the genus *Heterophrentis* and allied forms as a new subfamily, the Heterophrentinae, in which a strong cardinal fossula is developed and the axial structure of lobed septal ends is lost through the withdrawal of the septa from the axis in the ephebic stage. Neuman's (1969) work, however, suggests that both features are quite variable within streptelasmatid genera and the value of Kullmann's classification is regarded as questionable.

Of the Streptelasmatinae of Hill, *Ditoecholasma* has been placed in a new family by Sutherland (1965 : 35) and *Palaeophyllum* has been shown to belong to the Stauriidae (Hill 1961).

Genus *STREPTELASMA* Hall 1847

1847 *Streptelasma* Hall : 17.
?1930 *Streptelasma*; Smith : 311, *pars*.
1937 *Streptelasma*; Cox : 2, *pars*.
1958b *Brachyelasma*; Kaljo : 102.
1960 *Brachyelasma*; Pestana : 868.
1963b *Streptelasma*; Stumm : 25, *pars*.
1963 *Brachyelasma*; Ivanovskii : 42, *cum syn*.
1965 *Brachyelasma*; Ivanovskii : 62, 104.
1969 *Streptelasma*; Neuman : 8, *cum syn*.

Diagnosis. Solitary corals with a narrow peripheral stereozone and interseptal loculi present throughout ontogeny. Septa of two orders, the minor very short, the major usually extending more or less to the axis where the septal ends are irregularly twisted to form a weak axial structure. Major septa may be amplexoid in the ephebic stage. Tabulae complete and incomplete arched plates.

Type species (see Roemer 1861 : 19). *S. corniculum* Hall 1847 : 69, pl. 25, figs 1a–d. Trenton Limestone, Ordovician (Champlainian); Middleville, New York, U.S.A.

Discussion. Neuman (1969 : 10) has recently chosen and described a lectotype for *Streptelasma corniculum*. He showed that the type species of *Streptelasma* is congeneric with *Dybowskia prima* Wedekind (1927 : 18, pl. 1, figs 10, 11) (= *Brachyelasma primum*), the type species of *Brachyelasma*, and that the group of species up until then referred to *Streptelasma* required a new generic name. Neuman (1969 : 28) has erected the genus *Helicelasma* for these species.

Neuman (1969 : 9, fig. 3) recognized two groups of species within the genus *Streptelasma* thus emended, one characterized by amplexoid septa in the late neanic and ephebic stages, the other characterized by the persistence of loosely intertwined major septa in the axial region up to the immediately subcalicular level of the corallite. Both the type species of *Streptelasma* and its junior subjective synonym *Brachyelasma* fall into the ampleximorph group. Although Neuman claimed that intermediates exist between these two groups, he gave no details of these. In general, the two groups of species appear to be so well distinguished that the writer considers that separation at the subgeneric level may well prove to be justified.

Neuman (1969 : 7–8) also commented on the various subgeneric relationships previously suggested between these and other Ordovician members of the Streptelasmatidae. In particular, he regarded *Streptelasma* as emended and *Helicelasma* as warranting full separate generic status and this is followed here.

Streptelasma sensu Neuman is best known from the (?) Middle and Upper Ordovician to Llandovery of Scandinavia, the Baltic region and the U.S.S.R. The genus has also been recorded, usually as *Brachyelasma*, from the Upper Ordovician of Ireland (Kaljo & Klaamann 1965 : 421) and the Middle and Upper Ordovician of North America (Hall 1847 : 17; Pestana 1960 : 868).

Streptelasma shagami sp. nov.

(Pl. 2, figs 7–10; Text-fig. 6)

Derivation of name. After the collector of the type material, Dr R. Shagam (University of Pennsylvania).

Diagnosis. Conical corals reaching 26 mm diameter with 41 major septa. Skeletal elements unthickened throughout ontogeny and little stereoplasm developed. Major septa slim with some intermingling at the axis. Cardinal septum short in neanic stage, equal in length to other major septa in ephebic stage; weak fossula. Minor septa 2–4 mm long in basal calice. Tabulae well spaced, strongly arched in axis with flat or shallowly depressed crests.

Holotype. R46755 (S1583). Río Caparo, near the Paso Caparo; Silurian, Lower Llandovery.

Paratypes. R46756–9 (S1583), R46760 (K80748). Same locality and horizon as holotype.

Description. Incomplete conical corals embedded in matrix. Early ontogenetic stages unthickened. The peripheral stereozone is thin and highly longitudinally corrugated. The major septa are strongly pinnate, the longer septa meeting at the axis, the shorter ones leaning against the longer.

In the later neanic stages (Pl. 2, fig. 7), the peripheral stereozone is 0·5 mm or less in thickness. The septa are usually sinuous, occasionally straight, and variable in length although all reach or nearly reach the axis. They may be uniformly thick, about 0·25 mm, or slightly rhopaloid. There is some intermingling of the axial ends of the septa and they may fuse in groups of three or four: they may also be lightly invested with sclerenchyme in the axial area. The cardinal septum is shorter than the other majors, about a half the radius in length, in a poorly developed long narrow fossula. Rudimentary minor septa appear in the stereozone between most major septa. Horizontal elements are sporadic in the planes of section.

At the base of the calice (Pl. 2, figs 8, 10), the strongly grooved peripheral stereozone may reach 1 mm, and the septa 0·3–0·35 mm in thickness. Characteristically, the cardinal septum increases in length to equal the other major septa, although a weak fossula may still be detected—in the holotype (Pl. 2, fig. 8), the septa adjacent to the cardinal septum are shortened. Also, the counter septum shortens slightly and may only be a third of the radius in length. There is a slight withdrawal of the other major septa from the axis. Minor septa are short but well developed, < 2 mm long in the holotype but may reach 4 mm in the larger specimens. Traces of tabulae are scattered.

In longitudinal section (Pl. 2, fig. 9), tabulae are well developed, thin, complete or incomplete large curved plates. They are arranged as axial flat-topped or shallowly depressed domes sloping steeply downwards peripherally and developing narrow troughs against the wall in some instances. The arrangement in the axial area is obscured by septal traces. The tabulae are spaced 2–3 mm vertically apart. There are no dissepiments.

Ephebic stage sections of specimens in the type series show a great range in sizes from 11·8 to 26·3 mm mean diameter in calicular sections. Mature septal ratios range from 2·55 to 1·56 with increasing mean size. The data are shown graphically in Text-fig. 6.

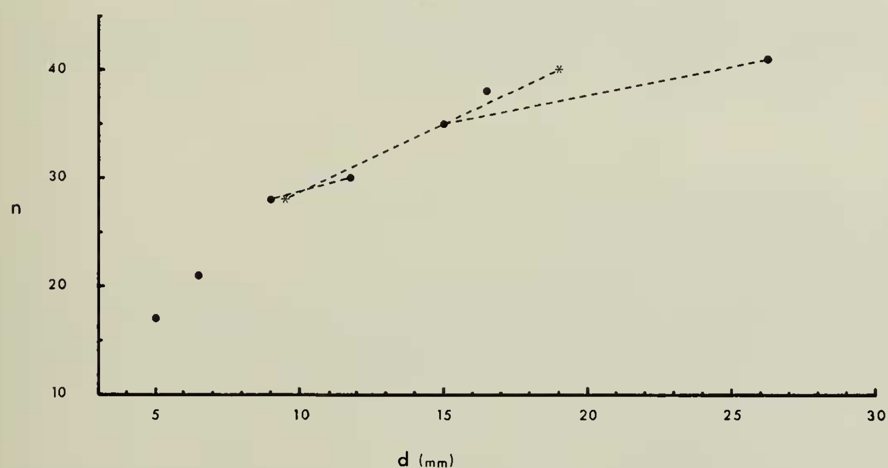

FIG. 6. Number of major septa plotted against diameter for specimens of *Streptelasma shagami*. The holotype is indicated by asterisks. The dashed lines join points representing different sections of the same specimen.

DISCUSSION. *Streptelasma shagami* has some similarity to *S. poulseni* Cox (1937 : 9) from the Richmondian (Ordovician) of Greenland. The Venezuelan species, however, is distinguished by its more strongly arched tabulae and a lower septal ratio.

Streptelasma sp.

(Pl. 2, figs 11, 12)

MATERIAL. R46761 (A2077). Río Caparo, near the Paso Caparo; Silurian, Lower Llandovery.

DESCRIPTION. The specimen is an incomplete conical coral, partly decorticated. In cross-section, the peripheral stereozone is 0·7 mm thick with well developed septal grooves. The major septa are short and thin, tapering gradually towards the axis. They are slightly less than half the radius in length. Only half of the corallite is seen in cross-section and in this neither a fossula nor any of the primary septa can be identified. The minor septa are very thin and variable in length, apparently extending axially as crests on the tabulae with a maximum axial extension of 2 mm. Tabulae are intersected, widely spaced, in the peripheral area.

In longitudinal section, the tabulae are thin and mainly incomplete. They are shallowly depressed across the axis and strongly domed in the peripheral area where subsidiary vesicular elements may occur. There is evidence of septal development on the crests of the tabulae. At the periphery, the plates may curve up slightly against the stereozone to form a small trough. In the axis, the spacing is somewhat irregular, averaging 7 tabulae in 10 mm.

There are an estimated 42 major septa at a diameter of 24 mm.

DISCUSSION. Despite the limits of the material, which preclude specific identification, this specimen can be confidently assigned to the genus *Streptelasma*.

Genus *LEOLASMA* Kaljo 1956

1956 *Leolasma* Kaljo : 36.
1965 *Leolasma*; Ivanovskii : 59.

DIAGNOSIS. Solitary conical corals. Septa of two orders, the major extending to the axis and dilated to completely close the lumen in early ontogeny. In mature stages, the major septa are dilated peripherally to form, with the minor septa, a moderately wide stereozone. Their axial ends are rhopaloid and fuse to form a more or less compact axial boss. Cardinal fossula narrow. Tabulae sparsely developed or absent.

TYPE SPECIES (by original designation). *Leolasma reimani* Kaljo 1956 : 36, pl. 9, figs 3–5. Upper Ordovician, Vazalemmaskii horizon; Rakvere, Estonia.

DISCUSSION. In his original diagnosis, Kaljo (1956 : 36) remarks that tabulae are absent and does not mention a cardinal fossula. Ivanovskii (1965 : 59), however, mentions sparse tabulae in his diagnosis for *Leolasma* and from published illustrations of *L. reimani* (Kaljo 1956, pl. 9, fig. 5; Ivanovskii 1965, pl. 2, figs 1a, b) a narrow cardinal fossula similar to that in the Venezuelan material appears to be present.

Leolasma appears to be very close to the genus *Kenophyllum* Dybowski which was revised by Kaljo (1958a : 22). Kaljo diagnosed *Kenophyllum* as lacking tabulae and, from his illustration of the type species *K. subcylindricum*, sclerenchyme is involved with the septa in the formation of the axial structure. Thus the present material compares more closely with *Leolasma* than *Kenophyllum* although the slight differences between the two may prove not to be of generic significance.

Leolasma is known from the upper Middle and lower Upper Ordovician of the Baltic area and China and is recorded here from the Lower Llandovery of the Mérida Andes.

Leolasma kaljoi sp. nov.

(Pl. 2, fig. 13; Pl. 3, figs 1–8; Text-fig. 7)

Derivation of name. After Dr D. L. Kaljo (Institute of Geology, Academy of Sciences of the Estonian S.S.R.).

Diagnosis. *Leolasma* with peripheral stereozone one quarter to one-third the radius. Cardinal fossula well developed with cardinal septum shortening rapidly in subcalicular stages. Tabulae simple, flat plates sloping axially and upwards, developed only in the ephebic stage: earlier stages completely infilled by laterally contiguous septa.

Holotype. R46762 (A2077). Río Caparo near the Paso Caparo; Silurian, Lower Llandovery.

Paratypes. R46763–7 (A2077), R46768 (A2079), R46769–75 (S1583). Same locality and horizon as holotype.

Description. Straight, conical corals reaching at least 30 mm high with a calice about 10 mm deep with steep sides and a shallow bowl shaped floor.

In the early stages (Pl. 3, fig. 6), the lumen is completely infilled by major septa reaching the axis, laterally contiguous along their whole length and alternating in the peripheral third to quarter of the radius with slim wedge shaped minor septa. The arrangement of the major septa varies between radial and slightly pinnate and a counter clockwise axial vortex may develop in some specimens.

The septa first separate in the cardinal fossula leaving a narrow elongate cavity bisected by a thin cardinal septum (Pl. 3, fig. 1). Subsequent spaces appear between major septa immediately on the axial side of the minor septa (Pl. 3, fig. 2). The major septa thin rapidly in their mid-length leaving a wide peripheral stereozone usually between a quarter and a third the radius wide, equivalent to the length of the minor septa, and an axial column of fused septal ends (Pl. 3, fig. 3). The septa in the axis are straight or a slight vortex may persist from earlier stages. Between the first separation of the septa and the base of the calice, the cardinal septum shortens rapidly and the axial column decreases in diameter and finally breaks up with the separation of the rhopaloid axial ends of the septa (Pl. 3, fig. 4). In the holotype, the cardinal septum decreases in length from 5 mm to 2·3 mm in 1·54 mm vertical growth and the major septa begin rapid withdrawal from the axis in the base of the calice about 3·5 mm above the level at which only a small cardinal fossula is open. In the calice, the peripheral stereozone is about one-third the radius in thickness except in the cardinal fossula where it is strongly notched. The cardinal septum is extremely short. The septal microstructure shows the water-jet pattern of divergent fibres typical of uniserial monacanthine trabeculae and is very well preserved in some specimens (Pl. 2, fig. 13).

Longitudinal sections are filled by septal tissue in which the trabeculae are directed axially and upwards at angles varying about 70° to the wall. Signs of tabulae are seen in one section only (Pl. 3, fig. 8) where complete flat plates 0·8 mm apart slope axially and upwards at about 30°.

Specimens range in size up to 17 mm in diameter with 38 major septa. Data are presented graphically in Text-fig. 7. Septal ratios range from 2·22 to 3·18 in mature sections.

Discussion. *Leolasma kaljoi* is distinguished from *L. reimani* Kaljo by the development of tabulae and the possession of a much stronger cardinal fossula. Otherwise, the two species appear to be very similar.

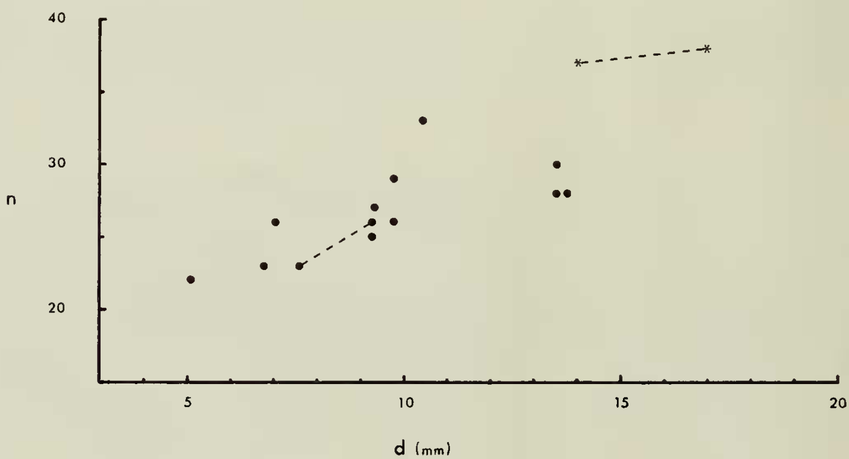

Fig. 7. Number of major septa plotted against diameter for specimens of *Leolasma kaljoi*. The holotype is indicated by asterisks. The dashed lines join points representing different sections of the same specimen.

Suborder COLUMNARIINA Rominger 1876

Family **SPONGOPHYLLIDAE** Dybowski 1873

1964 Spongophyllidae; Pedder : 436.

Discussion. The writer follows Pedder and others in considering the family Ptenophyllidae Wedekind 1923 as synonymous with the Spongophyllidae.

Genus ***CYMATELASMA*** Hill & Butler 1936

1936 *Cymatelasma* Hill & Butler : 516.

Type species. *Cymatelasma corniculum* Hill & Butler 1936 : 518, pl. 16, figs 2–8. Woolhope Limestone, Silurian, Wenlock; road cutting south of Stony Hill Farm, Woolhope, Herefordshire.

Diagnosis. Simple rugose corals with marked septal dilatation in early stages, usually reducing during ontogeny to a peripheral stereozone in the adult. The septa are waved parallel to their upper edges and carinae may develop along the crests of the waves. In the ephebic stage, the major septa are unequal in length and distinctively arranged in pinnate groups. Tabulae complete or incomplete: tabularium inversely conical or bowl-shaped. No dissepiments.

Discussion. Since Hill & Butler (1936) erected the genus and four species of *Cymatelasma* from beds of Llandovery to Ludlow age in the Welsh Borderland and the English Midlands, the genus appears to have been unused. Only passing comments on the genus are known to the writer.

Wang (1950 : 216), with no explanation, reassigned Hill & Butler's original species to *Pycnactis* (the type species), *Dinophyllum* and *Spongophylloides*. This dispersion seems completely unjustified as the genus from Hill & Butler's thorough descriptions appears to be a well defined homogeneous unit readily distinguished through septal structure, symmetry and lack of dissepiments from *Pycnactis* and *Dinophyllum*.

Cymatelasma is, however, most closely related to *Spongophylloides* and the species *Spongophylloides cockei* Sutherland (1965 : 16) includes in its range of variation specimens in which the dissepimentarium is almost completely replaced by a septal stereozone. Sutherland (*op. cit.*), in a useful comparison of the two genera, points out that they are distinguished only by the development of lonsdaleoid dissepiments in *Spongophylloides* and that *S. cockei* appears to show a continuous gradation between the two generic types. At present there is still some value in regarding the two genera as distinct and the Venezuelan species can be unequivocally assigned to *Cymatelasma*. If, however, *Spongophylloides pusillus* and *Cymatelasma carinatum* from the English Wenlock Limestone do prove to be a single variable species, a possibility suggested by Sutherland (*op. cit.*), then the status of *Cymatelasma* may need to be reconsidered.

Pedder (1967a : 3) remarked on the resemblances between *Cymatelasma*, *Enterolasma* and young individuals of *Lyrielasma*. *Lyrielasma* and *Cymatelasma* are undoubtedly closely related, the former genus differing essentially through the development of a dissepimentarium in later ontogeny, its exclusively (or nearly so) fasciculate growth form and a less consistently developed pinnate septal symmetry. It is possible that *Lyrielasma* is descended from *Cymatelasma* but the present known distribution patterns of the two genera do not encourage this suggestion.

The type species of *Enterolasma*, *E. strictum*, has never been adequately described and understanding of the genus is based chiefly on various accounts of *E. waynense* (Safford). *Cymatelasma* and *E. waynense* are superficially similar but the latter lacks a distinctive pinnate septal symmetry and possesses an arched tabularium similar to that in streptelasmatids.

The diagnosis given for *Cymatelasma* here is slightly modified from that given by Hill & Butler to take account of the new species. The South American record suggests that the distribution of *Cymatelasma* is far from adequately known and representatives of the genus are likely to be found in the Silurian of North America.

Cymatelasma aricaguaense sp. nov.

(Pl. 3, figs 9–15; Pl. 4, fig. 1; Text-fig. 8)

Derivation of name. After the type locality on the Río Aricagua.

Diagnosis. Ceratoid *Cymatelasma*. Major septa 36 at diameters of 11 to 14·5 mm, characteristically pinnate, lobed but not fused at their axial ends and bearing carinae sloping slightly axially and downwards. Tabulae incomplete; tabularium bowl-shaped.

Holotype. R46776 (A2558). Río Aricagua section; Silurian, Ludlow.

Paratypes. R46777–78 (A2558), R46779 (A2561), R46780 (A2562), R46781 (SC1). Same locality and horizon as holotype.

Description. Incomplete ceratoid corals with very weak septal grooves.

The peripheral stereozone is usually 1·5 to 2 mm but may reach 4 mm in thickness. Septa of two orders, the majors extending into the axial area but characteristically arranged and variable in length. The cardinal and counter septa are longest and almost join at the axis. The alar and the mid metasepta in the counter quadrants also nearly reach the axis, with the other septa shorter and arranged in pinnate groups in the six segments thus formed (Pl. 3, figs 9, 11, 12). The major septa are moderately thin, generally tapering slightly towards the axis but with small irregularities in thickness along their length. The sides of the septa bear small scattered thorny projections which are the sections of carinae sloping gently into the axis. The axial ends of the septa are usually lobed, often with thorns on the lobes, but they do not intermingle and only rarely do adjacent septa fuse. The swellings are usually larger on the axial ends of the cardinal and counter septa. The minor septa are variable in length but never project more than 0·5 mm beyond the peripheral stereozone. In late neanic–early ephebic sections, only rudimentary minor septa deep in the stereozone are present between some of the major septa (Pl. 3, fig. 12).

In longitudinal section, the stereozone is evenly developed from a minimum observed corallum diameter of 4 mm. Trabeculae are directed axially and upwards at 20–30° to the horizontal, becoming steeper towards the axis. The tabulae are mainly large incomplete curved plates, sloping into the axis steeply at the periphery but apparently with a flatter axial series. Their distribution is confused by the many septal traces and sections of the carinae. The lobed axial ends of the septa appear as a poorly defined spongy axial 'column'. In sections at right angles to their length, the septa appear strongly zigzagged with the carinae developed on the crests. On the sides of the septa the carinae are occasionally discontinuous along their length. They are otherwise regularly developed with an average vertical spacing of 0·5 mm and slope very gently into the axis.

The largest specimen is 14·5 mm in diameter with 36 major septa; the complete data are shown in Text-fig. 8. The septal ratio varies between 2·48 and 3·3 in maturity.

Discussion. *Cymatelasma aricaguaense* is immediately distinguished from all the species described by Hill & Butler through the possession of incomplete tabulae. Otherwise the Venezuelan species is most similar to *C. carinatum* Hill & Butler, although lacking the accelerated counter lateral minor septa of the latter. *C. aricaguaense* also has the characteristic septal symmetry more prominently developed than in *C. carinatum*.

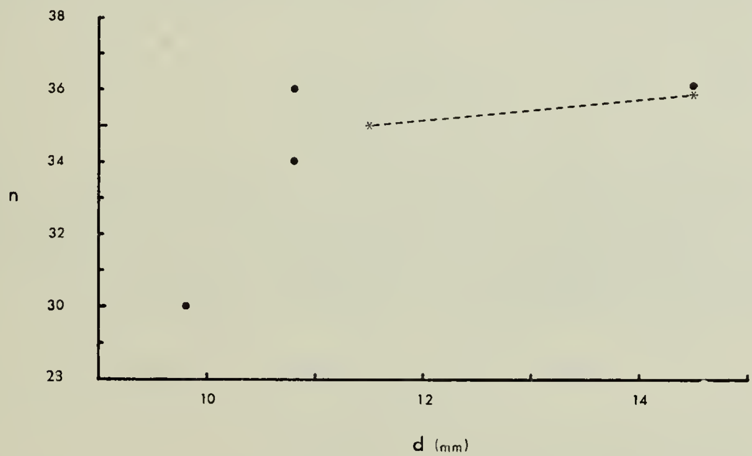

Fig. 8. Number of major septa plotted against diameter for specimens of *Cymatelasma aricaguaense*. The dashed line joins asterisks representing different sections of the holotype.

Suborder CYSTIPHYLLINA Nicholson 1889

Family **TRYPLASMATIDAE** Etheridge 1907

Genus ***TRYPLASMA*** Lonsdale 1845

1845 *Tryplasma* Lonsdale : 613.
1904 *Aphyllostylus* Whiteaves : 113.
1950 *Tryplasma*; Schouppé : 80.
1956 *Tryplasma*; Stearn : 91.
1961 *Tryplasma*; Strusz : 343.
1963a *Tryplasma*; Stumm : 4.
1963 *Tryplasma*; Oliver : 13 *cum syn.*
1964 *Tryplasma*; Stumm : 50.
1965 *Tryplasma*; Sutherland : 30.
1966 *Holacanthia* Sytova : 208.
1969 *Cantrillia*; Ivanovskii : 29, *pars.*
1969 *Holocanthia*; Ivanovskii : 31.
1969 *Tryplasma*; Ivanovskii : 33.
1969 *Rhabdacanthia* Ivanovskii : 45.
1969 *Wenlockia*; Ivanovskii : 52, *pars.*

Type species (by subsequent designation of Etheridge 1907 : 42). *T. aequabile* Lonsdale (1845 : 613, 633, pl. A, figs 7, 7a); Silurian, River Kakva, east side of northern Urals, U.S.S.R.

Diagnosis. Solitary and fasciculate rugose corals with acanthine septa and a narrow peripheral stereozone. Tabulae usually complete; no dissepiments.

Discussion. Ivanovskii (1969) has recently presented a comprehensive review of the Tryplasmatidae in which he advocated a series of generic divisions based on growth form and trabecular type. These two characters, however, appear in most cases in the tryplasmatids to be of doubtful genetic significance. The separation of solitary and fasciculate forms in the absence of other structural modifications seems inadvisable, particularly as species such as *T. malvernense* Hill show both growth forms. Further, the distinction between trabecular types is, at least to some extent, a function of preservation and holacanths may well be the recrystallized remains of original monacanthine or rhabdacanthine trabeculae. In both species of *Tryplasma* described here, rhabdacanths can be recognized in the septa where the microstructure is slightly better preserved although most trabeculae show varying degrees of alteration towards a holacanthine state. For these reasons, the genus *Tryplasma* is maintained here in the sense of earlier workers and the genera *Holacanthia* Sytova and *Rhabdacanthia* Ivanovskii are not recognized.

Tryplasma sp. cf. ***T. nordica*** Stumm 1963

(Pl. 4, figs 2–4)

cf. 1963a *Tryplasma nordica* Stumm : 4, pl. 2, figs 14–16.
cf. 1963 *Tryplasma nordica* Stumm; Oliver : 13, pl. 7, figs 1–7.

Material. R46782–4 (S1540A). Río Suripá section; Silurian, Ludlow.

Description. Cylindrical fragments of a *Tryplasma* with neither calice nor proximal end preserved nor any indication of increase.

The coral is subcircular in cross-section with a longitudinally corrugated epitheca reflecting septal grooves on the exterior. Diameters range between 5 and 5·5 mm with 22 major septa. The septa are discrete acanthine rhabdacanths, where the microstructure is preserved, embedded in lamellar calcite which forms a thin peripheral stereozone 0·3 mm thick (Pl. 4, fig. 4). Major and minor septa may be distinguished. Their appearance in cross-section is variable and occasionally the plane of section may fail to cut some or all of a ring of spines. The longest major septum seen was 0·7 mm long, the minor septa reaching up to half this length. Discontinuity or lobing of septa in cross-section due to the interception of two rhabdacanths in vertical series was occasionally seen.

In longitudinal section, the rhabdacanths are arranged on average 0·2 mm apart in regular vertical rows. The septa project into the lumen at a slightly variable but very low angle. The tabulae are usually complete and flat, although they may be slightly upturned peripherally. Occasionally incomplete tabulae slope steeply down into the axis. The tabulae are wide and irregularly spaced, averaging 1 mm apart. Dissepiments are not developed.

Discussion. The specimens agree more closely with the *T. nordica* from the Silurian (Wenlock or Ludlow) of Quebec described and figured by Oliver (1963) than with any other species of *Tryplasma*, particularly among those from North America. *T. nordica* is, however, larger with relatively, a somewhat lower septal number (48 to 60 septa of both orders in corals of 7·0 to 10·5 mm diameter according to Oliver) compared to the present material. The septa of the former are also longer and the tabulae more U-shaped. From Stumm's (1963a) description, the type specimens of *T. nordica* from the Silurian of Maine are less comparable to the Venezuelan specimens than Oliver's material.

Tryplasma sp.

(Pl. 4, figs 5–9)

Material. R46785 (S1540A). Río Suripá section; Silurian, Ludlow.

Description. Several small cylindrical corallites, well spaced and subparallel in a mudstone matrix, probably all belonging to one fasciculate colony.

The corallites are circular to subcircular, varying between 2·3 and 4·5 mm and averaging 2·8 mm in diameter. There are 19 major septa in a corallite 2·3 mm in diameter and about 28 in one 4·5 mm in diameter. The septa are acanthine rhabdacanths where details of microstructure can be observed. Their appearance in cross-section is highly variable and sometimes only one or two spines may be sectioned. They are set in lamellar calcite forming a peripheral stereozone 0·2–0·4 mm thick. Both major and minor septa may be distinguished, the latter reaching half the length of the former. The longest major septum seen in cross-section was 1 mm measured from the periphery.

In longitudinal section, the rhabdacanths project into the lumen with an elevation of 40°—there is little variation. One rhabdacanth measured 0·2 mm in diameter (Pl. 4, fig. 7). The septal spines are arranged 0·35 mm apart in vertical series. Tabulae are complete and flat or very slightly domed, their spacing varying between 0·4 and 1·7 mm. Dissepiments are not developed.

One instance of axial increase was seen in longitudinal section (Pl. 4, fig. 9). Only two daughter corallites were sectioned although more could be present out of the plane of section. In another corallite, a hysterocorallite was seen developing against the wall of the parent (Pl. 4, fig. 8). Whether this is a case of increase or an extreme form of rejuvenescence is uncertain.

Discussion. Among the several described species of *Tryplasma* which are fasciculate and have corallites of small diameter, *T. gracilis* (Whiteaves) and *T. lonsdalei* Etheridge appear to be the most similar to the present material. *T. gracilis* was redescribed by Stearn (1956 : 91, pl. 6, figs 1, 8) on weathered out but unsectioned topotype and other material from the Upper Ordovician Stonewall Formation of Southern Manitoba. It agrees with the specimens described here in size and growth form, including an apparent lack of connecting processes in the colony, but further comparison is difficult in the absence of sections of *T. gracilis*. Etheridge (1907) described several species of *Tryplasma* which have points in common with the Venezuelan material. Of these, the closest is *T. lonsdalei* var. *minor* Etheridge (1907 : 81, pl. 16, figs 3, 4; pl. 24, fig. 9; pl. 25, figs 6, 7; pl. 26, fig. 11), which has only slightly larger corallites and a comparable septal ratio to the Venezuelan material but differs from it by possessing connecting processes, slightly longer septa and more regular tabulae. Both Hill (1940 : 406) and Strusz (1961 : 343) agree in not differentiating Etheridge's varieties of *T. lonsdalei* and Hill describes rhabdacanthine septa in the species. In Australia, *T. lonsdalei* ranges in age from the Lower Devonian down to the Lower Silurian or Upper Ordovician.

At the present time, it is not possible to assign the Venezuelan coral to either *T. gracilis* or *T. lonsdalei* with confidence. A definite identification must await the collection of further material and more complete information on *T. gracilis*.

Order TABULATA Edwards & Haime 1850

Suborder FAVOSITINA Sokolov 1962

Family **COENITIDAE** Sardeson 1896

Genus ***COENITES*** Eichwald 1829

1829 *Coenites* Eichwald : 179.
1939 *Coenites;* Lecompte : 62.
1964 *Coenites;* Chudinova : 47.

Type species (see Miller 1897 : 727). *C. juniperinus* Eichwald 1829 : 179. Drift specimen, Lithuania (a neotype for *C. juniperinus* has been described from the Yagarakhuskii horizon (Wenlock); Saaremaa, Estonia by Klaamann 1964 : 116).

Diagnosis. Branching, laminar or finely zoned massive colonies. Corallites small and short, their walls thin proximally but much thickened distally, opening obliquely at the surface of the colony. Calices cresentic. Tabulae few and mural pores rare. Septa occasionally represented by three processes in the calice.

Coenites sp.

(Pl. 4, figs 10, 11)

Material. R46786 (S2275F). Río Suripá section. Silurian. Ludlow.

Description. A thin laminar encrusting colony 1·5 mm thick consisting of a single expansion which splits into two levels in one area.

Corallites about 0·1 mm across the short axis in longitudinal section, inclined at a low angle to the colony base and curving up slightly to meet the surface of the colony at an angle of 30–40°. Corallite walls thicken gradually from base to surface of the colony where they may reach 0·1 mm or slightly more in thickness. Mural pores are infrequent and about 0·05 mm diameter. The tabulae are flat, complete, variably spaced 0·25 mm or more apart.

The calices are gently curved, parallel sided slits with rounded ends 0·075 mm across and about 0·5 mm long. Septa are apparently not developed.

Discussion. This specimen may be referable to *Coenites laminatus* Hall (1852 : 143, pl. 39, figs 6a–d) which is widely recorded in rocks of Silurian age in North America. Unfortunately a modern description and adequate illustrations of the species are not available for a proper comparison to be made.

Suborder HALYSITINA Sokolov 1962

Family **HALYSITIDAE** Edwards and Haime 1850

Genus ***CYSTIHALYSITES*** Chernyshev 1941

1941 *Cystihalysites* Chernyshev : 70.
1962 *Cystihalysites*; Norford : 34.
1964 *Cystihalysites*; Sutton : 452, *cum syn.*

Type species. *Cystihalysites mirabilis* Chernyshev 1941 : 70, pl. 2, figs 5–7; pl. 3, figs 1–6. Upper Silurian; middle course of the Khandyga River, E. Verkhoyan'ya, U.S.S.R.

Diagnosis. Colonies formed of chains of long dimorphic corallites which divide and anastomose to form fenestrules. Autocorallites rounded or elliptical, sometimes developing septal spines and separated by rectangular mesocorallites. Tabulae of autocorallites usually complete, occasionally with vesicles on the corallite walls.

Tabulae of mesocorallites strongly arched or incomplete and vesicular. Autocorallites and mesocorallites separated by a true wall or peripheral faces of mesocorallite tabulae. Increase interstitial and peripheral. (After Sutton 1964 : 453).

Discussion. Nothing need be added here to the useful review of the genus given by Sutton (1964 : 452).

Cystihalysites brownsportensis (Amsden) 1949

(Pl. 5, figs 1–4)

1949 *Halysites catenularia brownsportensis* Amsden : 94, pl. 18, figs 1–3.
1955 *Halysites brownsportensis* Amsden; Buehler : 65, pl. 9, figs 4–6; pl. 10, fig. 6.
1957 *Cystihalysites brownsportensis* (Amsden) Hamada : 403, text-figs 1 (8), 2c.
1962 *Halysites brownsportensis* Amsden; Jull, text-fig. 1d.

Diagnosis. *Cystihalysites* with oval autocorallites 2 × 1·5 mm to 2·4 × 2 mm, developing short septal spines. Mesocorallites large, up to 1·5 mm long parallel to chain, containing small thin walled highly vesicular tabulae.

Material. R46787 (A2558), Río Aricagua section. R46788 (S2275F), Río Suripá section. Both Silurian, Ludlow.

Description. Damaged colonies, the largest piece 80 × 50 mm in area, composed of chains of dimorphic corallites. Crushing has broken the chains down to unbranched units up to 7 autocorallites in length. All signs of budding are extremely rare, suggesting large lacunae.

Autocorallites oval, internally smooth or weakly scalloped in cross-section. Internal diameters vary between 1·2 × 1·8 mm and 1·3 × 2·3 mm; external diameters 1·5 × 2 mm to 2·0 × 2·4 mm. Short septal spines are rarely seen (Pl. 5, fig. 3). The mesocorallites are large and square, 0·5 × 0·5 mm internally, or rectangular with the long axis, which may reach 1·5 mm internally, parallel to the chain. Auto- and mesocorallites are contained within a common wall varying between 0·15 and 0·3 mm thick and are separated by a thin partition 0·05 to 0·1 mm thick. There are no balken. Cross-sections of tabulae in the autocorallites are strongly curved and may even be circular. In the mesocorallites a thin walled network of vesicular tissue of about 0·2 mm diameter mesh and two to three ranks in width is developed. The autocorallites are spaced 2·7 to 3·9 mm centre to centre along the chains.

In longitudinal section the tabulae of the autocorallites are regularly developed, complete, arched, flat or saucer-shaped with few subsidiary plates. From colony to colony between 9 (rarely as few as 6) and 13 tabulae develop in 5 mm vertical growth. Traces of septal spines may be seen in subcentral sections developed in regular series 0·25 mm apart vertically. The mesocorallites are filled with thin walled, highly vesicular tabulae, usually 4 or 5 in 1 mm vertical growth and up to 6 ranks along the length of the chain in well developed mesocorallites. The wall separating auto- and mesocorallites is apparently formed by the thickened outer faces of the peripheral mesocorallite tabulae.

DISCUSSION. Apart from possessing very slightly larger autocorallites, the Venezuelan specimens agree in every respect with Amsden's and Buehler's figures and description of *Halysites brownsportensis*. This species is recorded from the Niagaran (Wenlock and Ludlow) of North America.

Genus *ACANTHOHALYSITES* Hamada 1957

1957 *Acanthohalysites* Hamada : 404.
1961 *Acanthohalysites*; Strusz : 353.

TYPE SPECIES. *Halysites australis* Etheridge 1898 : 78, pl. 17, figs 1–8. Silurian; Bell River, Wellington, N.S.W., Australia.

DIAGNOSIS. Dimorphic Halysitidae with septal spines developed in the autocorallites. Lacunae larger than autocorallites. Mesocorallites with non-cystose tabulae.

DISCUSSION. *Acanthohalysites* and *Cystihalysites* are distinguished only through the development of cystose tabulae in the mesocorallites of species of *Cystihalysites*; Hamada (1957 : 397) was unaware of the septal spines developed in that genus.

Acanthohalysites sp.

(Pl. 5, figs 5, 6)

MATERIAL. R46789 (S1540A). Río Suripá section; Silurian, Ludlow.

DESCRIPTION. Fragmental dimorphic chains 1·5 to 1·9 mm across up to 7 autocorallites in length unbranched. Shape and size of lacunae unknown.

The autocorallites are subcircular to strongly oval in cross-section with maximum internal dimensions of 1·8 × 1·3 mm. The internal face is often clearly scalloped and occasionally septal spines are seen well developed. The longest spine projects 0·25 mm into the lumen. In other autocorallite sections, spots of tissue in the lumen probably represent the tips of septal spines. Autocorallites and mesocorallites are enclosed by a common wall 0·2 to 0·3 mm thick within which they are separated by partitions also 0·2 to 0·3 mm thick. The mesocorallite lumen is very small, rectangular or circular, or it may be closed completely: its maximum size is about 0·45 × 0·25 mm, elongated across the width of the chain. The distance centre to centre between autocorallites along the chain is 2·2 to 2·6 mm.

In longitudinal section, the autocorallites contain complete, flat to saucer-shaped tabulae regularly spaced 13 to 15 in 5 mm vertical growth. Incomplete tabulae are extremely rare. In a subcentral section, regular series of septal spines are seen 0·15 to 0·25 mm apart vertically (Pl. 5, fig. 5, upper half of central corallite). The mesocorallites are very narrow and may be intermittently closed. The tabulae appear to be flat or saucer-shaped but their spacing is indeterminate.

Discussion. The Venezuelan specimen does not appear to be referable to an established species of *Acanthohalysites* but its indifferent preservation and fragmentary nature makes the erection of a new species undesirable.

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VII. APPENDIX—LOCATION OF SAMPLES

The following is the most accurate information available to the writer on the location of samples referred to in this paper. All the localities are in the southern Mérida Andes, western Venezuela. Sample numbers are prefixed 'A' for H. C. Arnold's collection, 'S' for R. Shagam's collection and 'K' for the collections of the Creole Petroleum Corporation. Location of the samples is also shown in Text-fig. 1.

Samples A1030, A1035 (Palmarito Formation, Permo-Carboniferous).

Section on the Quebrada Queveda (a tributary of the Río Mucuchachí) approximately 0·7 km due west of Portachuelo, Mérida State. A1030 is stratigraphically 0·5 m above the base of the Upper Palmarito limestone and A1035 is 45·5 m (including a break in the succession of 44 m which may conceal a fault) below the base of that limestone.

Samples A2077, A2079, S1583, K80748 (Caparo II, Lower Llandovery).

Section 10 to 15 m thick on the south bank of the Río Caparo at a pronounced bend in the river approximately 900 m downstream of the Paso Caparo, Mérida State. Locality 2 of Shell & Creole (1964, table 1).

Samples A2558–A2582, S1302, SC1, K162950 (Caparo IV, Ludlow).

Upper part of the Silurian section on the Río Aricagua, outcropping between approximately 4·1 km and 4·3 km upstream (measured direct) from the confluence of the Río Aricagua and the Río Caparo, Mérida State. Locality 7 of Shell & Creole (1964, table 1).

The equivalence between Arnold's collecting points (to which the measurements refer) and those of Shagam and Creole in the following table is approximate only.

Stratigraphic thickness in metres above base of Silurian outcrop:—

335		top of section	
			S1302
314	A2582		
308	A2579		
240·5	A2562		
237	A2561	≙	SC1, K162950
231	A2558		
0		base of section	

Sample 2722 (*Palmarito Formation, Permo-Carboniferous*).

213 m above the base of the Palmarito Formation in the Quebrada El Mesón, approximately 1·5 km west (measured direct) of its confluence with the Río Aricagua, Mérida State.

Samples S1540A, S2275D, S2275F (*Caparo IV, Ludlow*).

Upper part of a section approximately 550 m thick measured from the stratigraphic base at the major elbow in the upper reaches of the Río Suripá (see Text-fig. 1) downstream to a point, about 200 m above a tributary entering from the west, where the stratigraphically highest sample was collected (S1540A), Barinas State. Samples S2275D and S2275F are approximately 100–150 m below sample S1540A in the sequence.

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